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Inferring about the extinction of a species using certain and uncertain sightings

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ABSTRACT

The sighting record of threatened species is often used to infer the possibility of extinction. Most of these sightings have uncertain validity. Solow and Beet(2014) developed two models using a Bayesian approach which allowed for uncertainty in the sighting record by formally incorporating both certain and uncertain sightings, but in different ways. Interestingly, the two methods give completely different conclusions concerning the extinction of the Ivory-billed Woodpecker. We further examined these two methods to provide a mathematical explanation, and to explore in more depth, as to why the results differed from one another. It was found that the first model was more sensitive to the last uncertain sighting, while the second was more sensitive to the last certain sighting. The difficulties in choosing the appropriate model are discussed.

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1. Introduction

Mathematical models have become of importance for conservation scientists and policy makers since they offer a means to estimate the probability or likelihood that a species has gone extinct based on its historical sighting record (Jarić and Roberts, 2014; Solow, 1993; Solow and Beet, 2014; Thompson et al., 2013). The probability of extinction is an important quantity since it helps make informed decisions about conservation policies for threatened species. This could include deciding on whether to conduct expensive ecological surveys for the purposes of monitoring the species, and whether to continue other efforts to preserve a species. A flawed assessment could lead to failure in protecting a designated species.

The sighting record of a species compiles evidence of those years a species has been observed (although with varying degrees of uncertainty), and in some situations the record can extend over many decades. Rivadeneira et al. (2009) pointed out that statistical models that assessed the extinction status of species developed before 2009 were based on all sightings being valid with certainty. Roberts et al. (2010) showed that the inferences made from models that include uncertain sightings significantly differ from those omitting that information, and the conclusions about extinction were sensitive to the inclusion or exclusion of uncertain sightings. This led Solow et al. (2012) to develop a statistical method which treated uncertain sightings of the Ivory-billed Woodpecker in a formal way which neither simply treated them as valid nor excluded them. The limitation of the Solow et al. (2012) method is that it assumes that uncertain sightings occur only after the certain sightings, which is not generally the case in practice. Afterwards, Solow and Beet (2014) found a way to modify their method into two different probability models that allows overlap in time between certain and uncertain sighting.

Recently, several research groups have developed methods that take into account uncertainties and the actual strength of the evidence, by incorporating additional information, for example as to whether actual specimens of the species were recorded, or whether less certain video and/or audio recordings were collected, or whether there were just local verbal reports from experts or unreliable non-experts in some years (Lee, 2014; Thompson et al., 2017; 2013). This idea was then extended by assigning the probabilities of reliability to individual sightings (Jarić and Roberts, 2014; Lee et al., 2014). All of these models needed some expert (e.g Bird Life International) in the area to provide these sighting reliabilities and the inferences made from these models were sensitive to the sighting reliabilities. Because of the importance of these sighting reliabilities, Lee et al. (2015) developed a formal framework to elicit expert opinions in order to determine the validity of sightings. However, the model in Solow et al. (2012) and the two models in Solow and Beet (2014) differ from this approach. Solow et al. (2012) as well as Solow and Beet (2014) assume that certain sightings occur at a constant but unknown rate

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Fig. 1. Graphical representation of Ivory-billed Woodpecker sighting data. Green represents the years where there are certain sightings followed by pink which represents the uncertain sightings. Note the period of overlap. (For interpretation of the references to colour in this figure legend, the reader is referred to the web version of this article.)

and may be modeled as a Poisson process until extinction occurs. Uncertain sightings are considered as either valid or invalid and both valid and invalid sightings are also modeled as different Poisson point process with unknown rates (i.e Under Model 1 in Solow and Beet, 2014 the certain sighting rate is equivalent to the valid uncertain sighting rate). Thus both models in Solow and Beet (2014) and the model in Solow et al. (2012) do not need to rely on expert opinions, but on the other hand an underlying assumption that rates of certain and uncertain sightings, and valid and invalid sightings, are maintained in a reasonably homogeneous manner over time until extinction occurs.

Our main focus centers on the two models developed by Solow and Beet (2014). When these two models were used for inference about the extinction of the Ivory-billed Woodpecker, they gave very distinct results; one predicting the woodpecker is extant, and the other concluding that it is well and truly extinct. Here we examine the two extinction models of Solow and Beet (2014) and attempt to identify the factors that the models are most sensitive to. Because of the complexity of the two models it is not straightforward to identity these driving factors. This work is important as it gives insights into which factors require additional research for strengthening the knowledge base and thereby to reduce the uncertainties in the inferences made. Also we know that some prediction uncertainties can be reduced by additional data collection. Thus in situations where one model is more appropriate than the other, it is important to know which factor is most highly correlated with the model output before undertaking expensive studies to gather and analyze additional data.

2. Data

As a first step, it is of interest to examine the sighting record data of the Ivory-billed Woodpecker reported in Roberts et al. (2010). Following Solow and Beet (2014), we treated all sightings not based on physical evidence as uncertain. Since there was no natural way to define the beginning of the observation period, the period was taken to be (1897,2010) and the first sighting in 1897 was omitted as per the most methods in literature (Boakes et al., 2015; Solow, 1993; Solow and Beet, 2014). The record period from 1897 to 2010 contains 21 certain sightings in years 1898–1902, 1904–1910, 1913, 1914, 1917, 1924, 1925, 1932 1935, 1938, and 1939 and 46 uncertain sightings in years 1911, 1916, 1920, 1921, 1923, 1926, 1929–1931, 1933, 1934, 1936, 1937, 1941–1944, 1946, 1948–1952, 1955, 1958, 1959,1962, 1966–1968, 1969, 1970–1974, 1976, 1981, 1982, 1985–1988, 1999, 2004–2006, where for example 2004–2006 means that there are sightings in every year from 2004 to 2006. The Ivory-billed Woodpecker sighting data described above, is visualized graphically in Fig. 1.

In what follows, we adopt an unconventional format and provide the Methods and then give results first for Model 1, and then follow this for Model 2.

3. Methods-Model 1

We begin by outlining the basic structure of the first model of Solow and Beet (2014). Define the observation period of a species as $(0, T)$, where 0 is the time when observations began and the period lasts for T years altogether. The complete sighting record $t = (t_1, t_2, \ldots, t_n)$ consists of the times (i.e., here the years) when the species were sighted during the observation period.

If the sighting is based on clear physical evidence, it is classified as certain; but if it is classified by a sound recording, photograph or video, or some other less precise confirmation, it is classified as uncertain. Thus, for observed data, we only know whether each sighting is certain or uncertain. All certain sightings are considered to be valid. Note, however, that uncertain sightings can either be valid or invalid. In practice, whether an uncertain sighting is valid or invalid is often unknown.

In the datasets studied here, all that is known is which sightings are certain and which are uncertain. From this information, the rates of valid and invalid sightings can be inferred, so that an informed decision can be made as to the likelihood of the species being extant or extinct.

Under the first model of Solow and Beet (2014), the sighting record is divided into two parts with the division based on the (unknown) extinction time τ_E. Over the first time period in the interval $(0, \tau_E)$, valid sightings follow a stationary Poisson process with rate Λ, and invalid sightings follow a stationary Poisson process with rate Θ. The expected proportion of valid sightings is $\Omega = \Lambda/(\Lambda + \Theta)$. Then, the invalid rate Θ is equal to $[(1 - \Omega)]/\Omega$.

Over the second time period in the interval (τ_E, T), all the sightings are invalid and follow a stationary Poisson process still with rate Θ. That is, the rate of invalid sighting does not change over the whole interval $(0, T)$. Model 1 is summarized in Fig. 2.

Let n_c and n_u be the number of certain and uncertain sightings. The first model proceeds by assuming the extinction time τ_E falls in the interval $(0, T)$, with $n(\tau_E)$ sightings prior to τ_E. We suppose the number of valid uncertain sightings in $(0, \tau_E)$ is the random variable j. This gives the scheme shown in Fig. 2. There are thus $n_c + j$ valid sightings in $(0, \tau_E)$, and there are $n - (n_c + j)$ invalid sightings in $(0, T)$. The goal is to construct likelihoods for the valid and invalid sightings in these two time intervals, and assess the extinction hypothesis from these likelihoods.

In more detail, let E be the event that the species became extinct during the observation period $(0, T)$ and $\bar{\mathrm{E}}$ be the event that the species is extant at time T. By Bayes theorem, the posterior probability of an extinction event E given the complete sighting record t is

$$p(E|t) = \frac{p(t|E)p(E)}{p(t|E)p(E) + p(t|\bar{\mathrm{E}})(1 - p(E))}, \tag{1}$$

where $p(t|E)$ is the likelihood of t given E, $p(t \mid \bar{\mathrm{E}})$ is the likelihood of t given $\bar{\mathrm{E}}$, and $p(E)$ is the prior probability of extinction.

The Bayes factor $(B(t))$ is a standard Bayesian measure that is used to make a decision of whether the data support the null hypothesis E, that the species went extinct in the study interval, while not depending on $p(E)$. Then the Bayes factor is defined as:

$$B(t) = \frac{p(t|E)}{p(t|\bar{\mathrm{E}})}. \tag{2}$$

A value of $B(t) > 3$ constitutes substantial evidence for the null hypothesis E, while a value $B(t) < 1/3$ constitutes substantial evidence for the alternative hypothesis $\bar{\mathrm{E}}$ that the species is extant (Kass and Raftery, 1995; Solow and Beet, 2014). In the following section, we will describe methods for estimating the Bayes Factor, so that the null hypothesis may be tested with real sighting data.

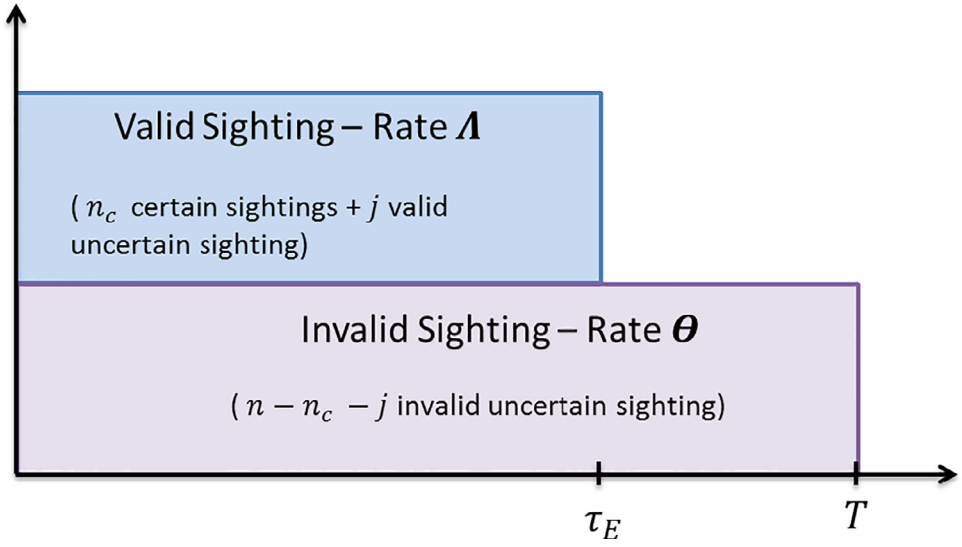

Valid Sighting – Rate Λ
(n_c certain sightings + j valid uncertain sighting)
Invalid Sighting – Rate Θ
($n - n_c - j$ invalid uncertain sighting)
τ_E
T

Fig. 2. Model 1 is based on the assumption that the valid and invalid sightings follow different Poisson process. The species becomes extinct at time τ_E. Before τ_E, all sightings are either valid with rate Λ or invalid with rate Θ. In the real data all certain sightings are valid, while uncertain sightings are either valid or invalid. After the species becomes extinct at time τ_E, all sightings must be invalid with rate Θ, and appear in the real data as uncertain.

The likelihood $p(t|E)$ is given by

$$p(t|E) = \int_{t_L}^{T} p(t|\tau_E)p(\tau_E)d\tau_E, \tag{3}$$

where $p(t|\tau_E)$ is the likelihood of t given that extinction occurs at time τ_E and $p(\tau_E)$ is the prior probability density function of the extinction time. The time point t_L is the last certain sighting which makes $p(t|\tau_E) = 0$ if $\tau_E < t_L$. Also the likelihood $p(t|\bar{E})$ is given by

$$p(t|\bar{E}) = p(t|\tau_E = T). \tag{4}$$

The likelihood of t given τ_E for Model 1 can be obtained from Solow and Beet (2014) through a set of calculations and assumptions on model parameters.

$$p(t|\tau_E) = \int_0^1 \omega^{-n_u}(1-\omega)^{n-n(\tau_E)}(n-1)!(\tau_E + (\frac{1-\omega}{\omega})T)^{-n}d\omega. \tag{5}$$

Note that in Eq. (5) the proportion of valid sightings Ω runs over different values of ω. Eq. (5) can then be combined with a specified prior pdf $p(\tau_E)$ to find the corresponding posterior distribution and hence $p(t|\bar{E})$ and $p(t|E)$ as follows,

$$p(t|\bar{E}) = p(t|\tau_E = T) = \frac{(n-1)!}{T^n}\int_0^1 \omega^{n_c}d\omega = \frac{(n-1)!}{T^n(n_c+1)}, \tag{6}$$

$$p(t|E) = \int_{t_L}^{T} p(t|\tau_E)p(\tau_E)d\tau_E. \tag{7}$$

We build our study based on Eqs. (6) and (7) which were formulated in Solow and Beet (2014). In our study here, we assume a uniform distribution $p(\tau_E) = \frac{1}{T}$ on $0 \le \tau_E \le T$ and change variables to $x = \frac{\tau_E}{T}$, then some cancellations occur resulting in a simplified Bayes Factor (BF):

$$BF_1 = \frac{p(t|E)}{p(t|\bar{E})} = (n_c+1)\int_\epsilon^1\int_0^1 \omega^{n_c-n}\frac{(1-\omega)^{n-n(xT)}}{(x+\frac{1}{\omega}-1)^n}d\omega dx, \tag{8}$$

where $\epsilon = \frac{t_L}{T}$.

If we let $I(\omega, x) = \omega^{n_c-n}\frac{(1-\omega)^{n-n(xT)}}{(x+\frac{1}{\omega}-1)^n}$, we get the following as the Bayes factor corresponding to the Model 1:

$$BF_1 = (n_c+1)\int_\epsilon^1\int_0^1 I(\omega, x)d\omega dx. \tag{9}$$

At the first glance, Eq. (9) suggest that BF_1 will be strongly depend on n_c and ϵ but by closely observing $I(\omega, x)$ it is clear that it also depends on the order of the actual data through $n(xT)$. Note that $n(xT)$ is the number of sightings prior to time xT.

4. Results-Model 1

There is no closed form solution for the Bayes factors BF_1 Eq. (9) in Model 1, and it can only be solved through numerical integration. As such, one cannot clearly see which variables BF_1 is most sensitive to. In what follows we attempt to identify the key influential variables.

Using Eq. (8), the Bayes factor was calculated for a number of different versions of the woodpecker dataset (see Data above). Note that the Ivory-billed woodpecker data is characterized by a period of certain sightings followed by a period of uncertain sightings, and at the cross-over point there is a small period of overlap where there are both certain and uncertain sightings (see Fig. 1). Hence we found it useful to examine the sensitivity of Model 1 to certain and uncertain sightings separately. In order to achieve this we considered different variations of the original sighting data of Ivory-billed Woodpecker. The Left Hand (LH) graph of Fig. 3 examines the Bayes Factor when changing certain sightings in the dataset, while the Right Hand (RH) graph examines the Bayes Factor when changing uncertain sightings in the dataset. When changing the certain sighting information we deleted the last certain sighting sequentially, and calculated the Bayes Factor each time. Thus where the x-axis indicates 1932/18, this refers to the last certain sighting being in 1932 and the total number of certain sightings being $n_c = 18$. In a similar manner we changed the uncertain sighting information as well.

By comparing the magnitudes of the two graphs in Fig. 3 it is clear that the Bayes Factor for Model 1 changes significantly in the RH graph and thus controlled by the uncertain sightings. The magnitude of the RH graph can reach values of BF $\sim 10^6$ (i.e., orders of magnitude higher than left graph) which gives overwhelming evidence that Model 1 is much more sensitive to uncertain sightings.

Note that the RH graphs in Fig. 3 examines two parameters (i.e. the number of uncertain sighting and the last uncertain sighting) as they are changed simultaneously. In order to investigate which parameter is the most influential we need to keep one parameter fixed while changing the other. We therefore considered two situa-

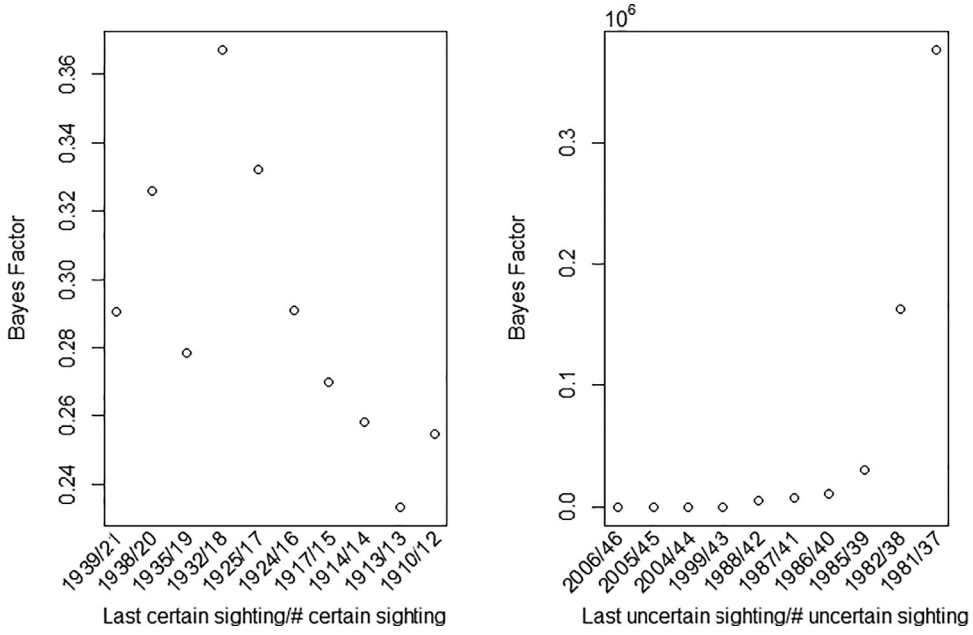


Fig. 3. LH graph. Change in the Bayes factor for Model 1 for different variants in certain sightings. When the x-axis indicates 1932/18, this refers to the last certain sighting being in 1932 and the total number of certain sightings being $n_c = 18$. RH graph is the same, but for uncertain sightings. Note that the magnitudes observed in the RH graph is 10^6, indicating Model 1 is much more sensitive to uncertain sightings.

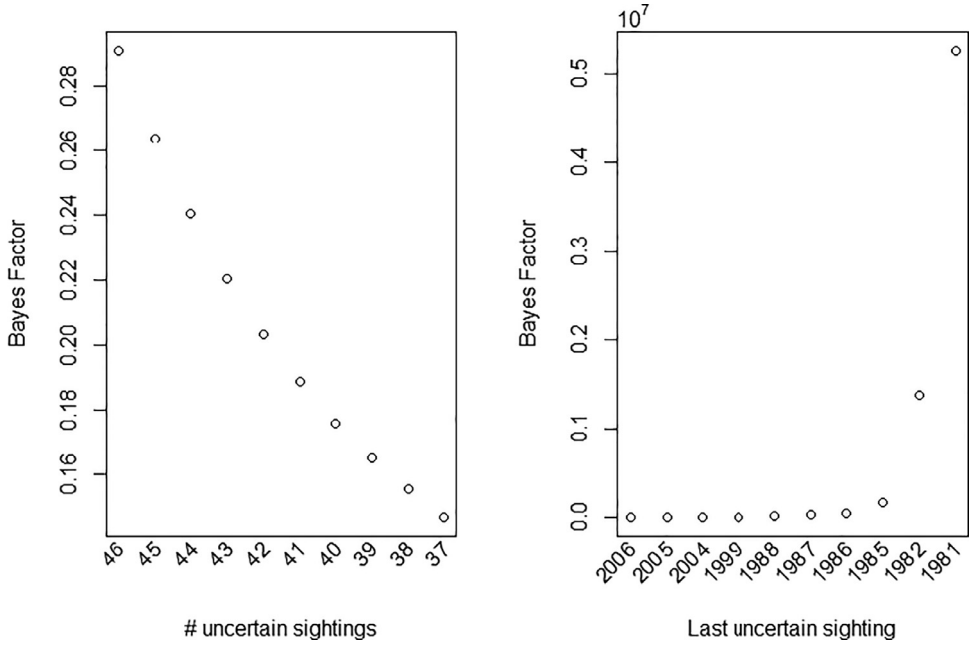


Fig. 4. Change in the Bayes factor for Model 1 for different variants in uncertain sightings. Note that the magnitude of that RH graph is 10^7. Comparing the LH and RH graphs it gives evidence that Model 1 is much more to the last uncertain sighting than to the number of uncertain sightings.

tions in Fig. 4; one having the last uncertain sighting fixed at 2006 and the other having the same fixed number of uncertain sightings as the original data.

By examining the graphs in Fig. 4 it becomes evident that the change in the last uncertain sighting (rather than number of uncertain sightings) is largely responsible for the huge changes in the Bayes Factor for Model 1. Hence our working hypothesis for Model 1 is that the Bayes Factor is most sensitive to the last uncertain sighting. Given the structure of Model 1, this seems a reasonable prediction. This is because Model 1 assumes that the all valid sightings, whether certain or uncertain follows the same Poisson process. In this case, the relatively high rate of certain sightings prior to 1939 ensures the rate of valid sightings prior to 1939 is large. Since the same rate will be applied to valid uncertain sightings after 1939, this implies the majority of uncertain sightings are valid, and thus extinction occurs immediately after the last uncertain sighting. Hence the value of BF_1 will start to favor the hypothesis that the extinction occurred between (0, T), and more as the gap increases between the last uncertain sighting and T.

4.1. The importance of the last uncertain sighting

In order to understand the Bayes Factor better, we examined its behavior under a number of simplified scenarios that gave some analytical insights.

Case 1: Model 1. No extinction baseline

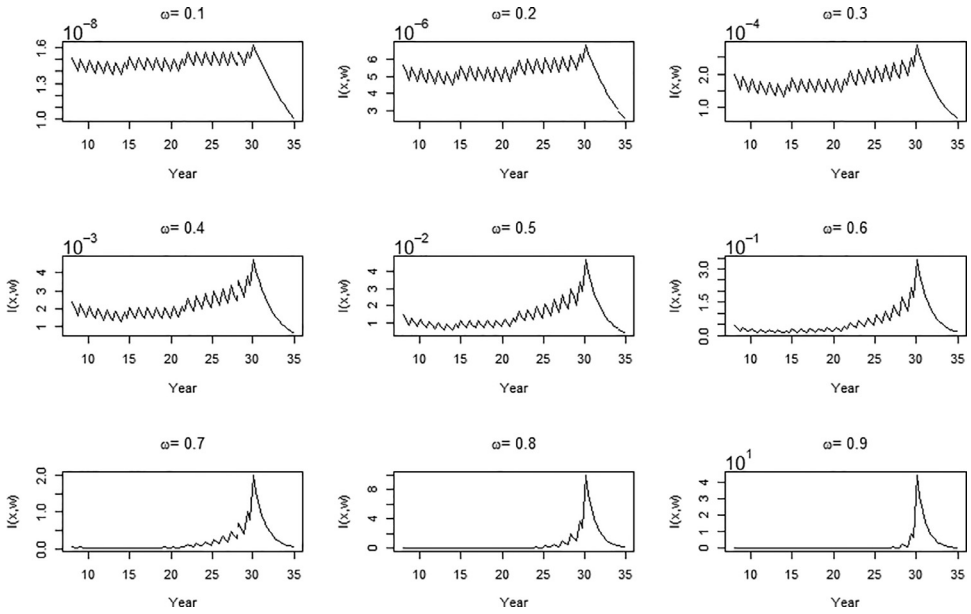


Fig. 5. $I(\omega, x)$ is plotted as a function of time for different fixed values of ω when sightings are homogeneous. Here ω is the expected proportion of valid sightings and $I(\omega, x)$ is the integrand in Eq. (9) which is used to calculate the Bayes factor for Model 1. $I(\omega, x)$ has major peaks at the last uncertain sighting and the peak gradually increases when ω is increased.

First, it was assumed that all sightings are spread uniformly until the end of the observation period T. This would correspond to a baseline scenario of what we would expect if the species never went extinct,when all valid sightings had the same rate in $(0, T)$.

In such a case, the number of sightings in the interval $(0, xT)$ could be approximated by $n(xT) = nx$, for $0 \le x \le 1$. For this case, Eq. (8) can be simplified to

$$BF_1 = (n_c+1)\int_\epsilon^1 \int_0^1 \omega^{n_c-n}\frac{(1-\omega)^{n-n(xT)}}{(x+\frac{1}{\omega}-1)^n}d\omega dx$$
$$= (n_c+1)\int_0^1 \omega^{n_c}\left(\frac{1-\omega}{\omega}\right)^n \int_\epsilon^1 \left(\frac{(1-\omega)^{-x}}{(x+\frac{1}{\omega}-1)}\right)^n dx d\omega. \quad (10)$$

Laplace's method is used to approximate integrals of the form $\int_a^b \exp(Mf(x))dx$ (Laplace, 1986). The method requires that the value of M should be large and $f(x)$ should be a twice-differentiable function. The integral over x in Eq. (10) can be evaluated using Laplace's method as $\frac{(1-\omega)^{-x}}{(x+\frac{1}{\omega}-1)}$ is twice differentiable. In this special case, the maximum of the integrand occurs at the end point $x = 1$, where in general for large n

$$I_n = \int_\epsilon^1 \exp(ng(x))dx \sim (ng'(1))^{-1}\exp(ng(1)). \quad (11)$$

Using Eq. (10) and $-\log(1-\omega) = \omega + \frac{\omega^2}{2} + \frac{\omega^3}{3}\ldots$. we obtain,

$$BF_1 \approx (n_c+1)\int_\epsilon^1 \omega^{n_c}\left(\frac{1-\omega}{\omega}\right)^n\left[\left(\frac{\omega}{1-\omega}\right)^n \times \frac{2}{n\omega^2}\right]$$
$$d\omega = \frac{2}{n}\left(\frac{n_c+1}{n_c-1}\right) \quad (12)$$

For large n_c Eq. (12) is approximately equal to $2/n$. It is also clear that the value of BF_1 will always be less than 3, which simply mean that the species will always be extant if sightings are spread uniformly until the end of observation period. This is to be expected because according to Model 1, the latter conforms exactly to the alternative hypothesis that the species is extant.

From Eq. (12) it is also seen that for $n_c > 10$, the certain sightings do not play a significant role when making inferences about extinction for Model 1. This can also be observed in Fig. 3 where the Bayes factor does not change significantly upon the deletion of certain sightings. These results imply that Model 1 inference is very much influenced by when the last uncertain sighting occurred. The next section illustrates this idea through a simple example.

Case 2: Last uncertain sighting $t_n < T$

Consider Model 1 for the specific case when uncertain sightings terminate before the end of the observation period. As a typical example, consider a simulated time series of sightings where the last uncertain sighting occurs at $t = t_n$, and the uncertain sightings are distributed uniformly in the interval $(0, t_n)$. The results obtained can be generalized to any number of certain and uncertain sightings but in order to present numerical results it will be assumed that there are certain sightings in every year from 1 to 8 (1–8) and uncertain sightings from year 5 to 30 (5–30) for the 35 years of the observation period.

The main contributions to the Bayes Factor in Eq. (9) can be found from examining the integrand for $I(\omega, x)$ of the integral in Eq. (9). Fig. 5 illustrates some plots of the integrand $I(\omega, x)$ at fixed values of ω, as a function of time x.

Fig. 5 makes clear that for $\omega > 0.6$, the integrand has a major peak orders of magnitude higher than 2 and it is exactly located at the last uncertain sighting (t_n) not before or after it. ω is the expected proportion of valid sightings and Fig. 5 illustrates that $I(\omega, x)$ has comparatively large values when ω is large or generally Model 1 treats most uncertain sightings to be valid. Hence the distance between the last uncertain sighting and the observation end period will determine the value of BF_1. This property makes Model 1 conclude that the species is extinct only if the last uncertain sighting and the observation end period is away from one another. By doing further numerical calculations for this particular example it was found that the species can be inferred to be extinct if the last uncertain sighting and the observation end period is away from one another by at least five years.

The steep peak at the last uncertain sighting after a specific value of ω can be explained by the following property.

$$\lim_{n\to\infty} a^n = \begin{cases} 0, & \text{if } a < 1 \\ \infty, & \text{if } a > 1 \end{cases} \quad (13)$$

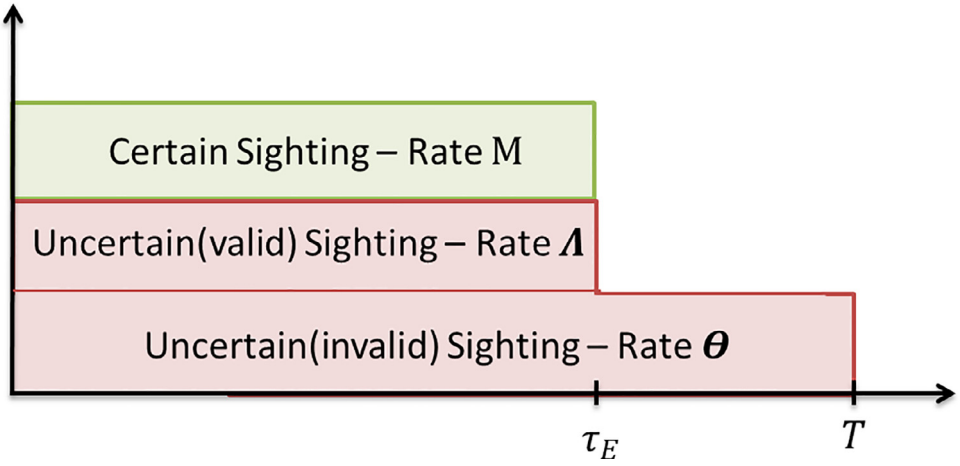


Fig. 6. The basis of Model 2 is developed on the fact that the certain and uncertain sightings follow different Poisson process. The species becomes extinct at time τ_E. Before τ_E, all sightings are either certain with rate M or uncertain(valid with rate Λ; invalid with rate Θ). After the species becomes extinct at time τ_E, all sightings must be uncertain(invalid) with rate Θ.

When $x = \frac{t_n}{T}$ and $n(xT) = n$, we get

$$BF_1 = (n_c+1)\int_\epsilon^1\int_0^1 \omega^{n_c-n}\frac{(1-\omega)^{n-n(xT)}}{(x+\frac{1}{\omega}-1)^n}d\omega dx$$
$$= (n_c+1)\int_\epsilon^1\int_0^1\left[\frac{\omega^{n_c/n}}{\omega\left(\left(\frac{t_n}{T}\right)+\left(\frac{1}{\omega}\right)-1\right)}\right]^n d\omega dx. \quad (14)$$

By virtue of Eq. (13), the steep peak will initiate when $\omega = \omega_1$, where ω_1 satisfies the following

$$\omega_1^{\frac{n_c}{n}} = \omega_1\left(\left(\frac{t_n}{T}\right)+\left(\frac{1}{\omega_1}\right)-1\right) \quad (15)$$

Solving Eq. (15) for our data it was found that $\omega_1 = 0.66$.

By observing Fig. 5, it is clear that the steep peak at the last uncertain sighting starts to increase rapidly after ω is greater than 0.66. There is also a peak at $t_(n-1)$ but it is comparatively very small, as shown in the Appendix A.

We just considered the case where uncertain sightings are distributed uniformly in time but the last uncertain sighting abruptly ends sometime before T. Model 1 would then predict a major peak in $I(\omega, t)$ at the last uncertain sighting, the BF_1 will accordingly be large, and extinction predicted.The same idea can be generalized for non-uniformly distributed data, which is described in the Appendix A.

5. Methods- Model 2

Under the second model it is assumed that certain sightings follow an independent Poisson process with rate M, while valid uncertain sightings follow a stationary Poisson process with rate Λ and invalid sightings follow a stationary Poisson process with rate Θ. In this situation, certain sightings differ qualitatively from valid sightings that are uncertain. Also, Model 2 assumes certain and uncertain sightings to be independent of each other. Fig. 6 provide a summary of Model 2.

Let t_c and t_u denote the sets of certain and uncertain sightings respectively. The conditional likelihood of the complete set of sightings given τ_E is the product of

$$p(t|\tau_E) = p(t_c|\tau_E)p(t_u|\tau_E), \quad (16)$$

where $p(t_c|\tau_E)$ is the likelihood of t_c given τ_E and $p(t_u|\tau_E)$ is the likelihood of t_u given τ_E. Augmenting a non-informative prior pdf for $p(\mu) = \frac{1}{\mu}$ on $0 \le \mu \le \infty$, for M, a development parallel to Model 1 yields:

$$p(t_c|\tau_E) = \frac{(n_c-1)!}{\tau_E^{n_c}}, \quad (17)$$

and

$$p(t_u|\tau_E) = \int_0^1 (n_u-1)!\omega^{-n_u}(1-\omega)^{n_u-n_u(\tau_E)}\left(\tau_E+\left(\frac{1-\omega}{\omega}\right)T\right)^{-n_u}d\omega, \quad (18)$$

where $n_u(\tau_E)$ is the number of uncertain sightings prior to τ_E. Eq. (18) can be obtained by replacing n by n_u in Eq. (5). Note that Eq. (18) differs from Solow and Beet (2014) by a term $(n_u-1)!$. The term $(n_u-1)!$ is needed when working with the exact likelihood.

Hence we obtain the following:

$$p(t|\tau_E) = \frac{(n_c-1)!(n_u-1)!}{\tau_E^{n_c}}\int_0^1 \frac{\omega^{-n_u}(1-\omega)^{n_u-n_u(\tau_E)}}{\left(\tau_E+\left(\frac{1-\omega}{\omega}\right)T\right)^{n_u}}d\omega, \quad (19)$$

Eq. (19) can then be combined with a specified prior pdf $p(\tau_E)$ to find $p(t|\bar{E})$ and $p(t|E)$as follows:

$$p(t|\bar{E}) = p(t|\tau_E = T) = \frac{(n_c-1)!(n_u-1)!}{T^{n_c}T^{n_u}}, \quad (20)$$

$$p(t|E) = \int_{t_L}^T p(t|\tau_E)p(\tau_E)d\tau_E. \quad (21)$$

If we assume a uniform distribution $p(\tau_E) = 1/T$ on $0 \le \tau_E \le T$ and change variables to $x = \tau_E/T$, then some cancellations occur resulting in a simplified Bayes Factor (BF):

$$BF_2 = \frac{p(t|E)}{t|\bar{E}} = \int_\epsilon^1\int_0^1 \frac{(1-\omega)^{n_u-n_u(xT)}}{\omega^{n_u}x^{n_c}(x+\frac{1}{\omega}-1)^{n_u}}d\omega dx, \quad (22)$$

Let $I'(\omega, x) = [(1-\omega)^{n_u-n_u(xT)}]/[\omega^{n_u}x^{n_c}(x+\frac{1}{\omega}-1)^{n_u}]$. Thus, we obtain the following as the Bayes factor corresponding to the Model 2:

$$BF_2 = \int_\epsilon^1\int_0^1 I'(\omega, x)d\omega dx. \quad (23)$$

6. Results- Model 2

Similar to BF_1 , BF_2 can only be solved through numerical integration. In order to identify the variables which most influence the

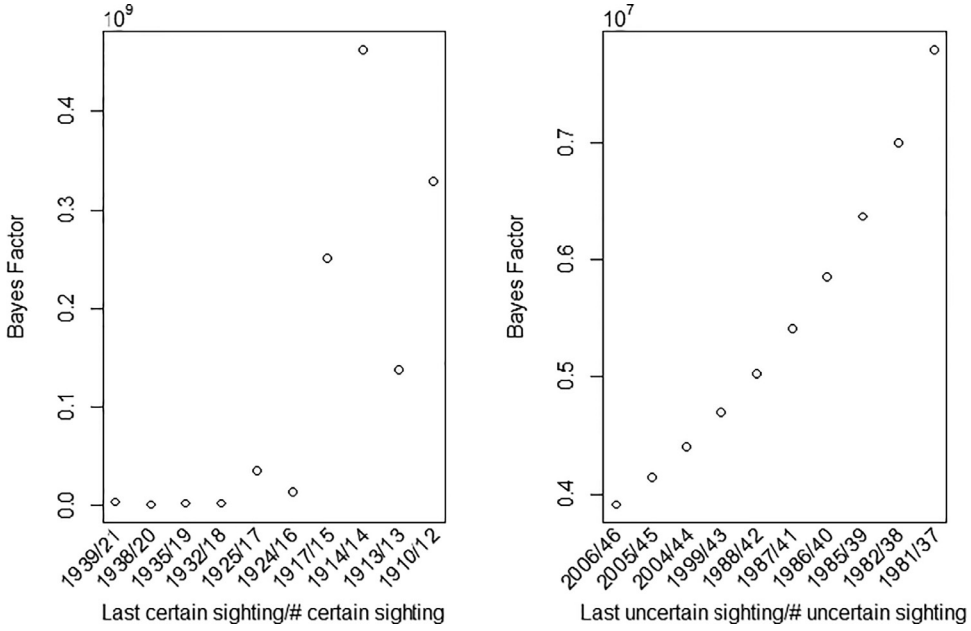


Fig. 7. Change in Bayes factor for Model 2 for different variants in both certain and uncertain sightings. Note that the magnitude of the LH graph is 10^9, which gives evidence that Model 2 is much more sensitive to certain sighting.

value of BF_2, we first checked which sighting type (i.e certain or uncertain) dominates more under model 2. Hence we considered the same variants as in Fig. 3.

According to Fig. 7 it is clear that the Bayes factor for Model 2 changes significantly in the LH graph. Once again to investigate which parameter (i.e. the last certain sighting or the number of certain sightings) dominates more, we consider the situations in Fig. 8. The RH graph of Fig. 8 has the last certain sighting fixed at 1939 and the left graph has the same fixed number of certain sightings as the original data.

Comparing the graphs in Fig. 8 it becomes evident that the change in the last certain sighting was responsible for the huge changes in Bayes factor for Model 2. Hence Model 2 is particularly sensitive to the last certain sighting, and this became our working hypothesis for Model 2.

We can again use Laplace's method to obtain a general idea about the integral in Eq. (23) but now the factor x^{-n_c} moves the maximum of the integrand to the end point $x = \epsilon$ (rather than $x = 1$ for BF_1). The remaining integral over ω is solvable but from the Mean Value Theorem, we can express the integral as the value of the integrand at some point $\overline{\omega} \in (0, 1)$. To get a feel for the order of magnitude of BF_2 take $\overline{\omega} = 0.5$. Combined with Laplace method using $n_u(xT) = n_u x$, we obtain the asymptotic estimate,

$$BF_2 \approx \frac{(0.5)^{n_u\epsilon}}{n_u \epsilon^{n_c}(\epsilon+1)^{n_u}}. \tag{24}$$

Even though the result in Eq. (24) does not simply explain the situation as clearly as in BF_1, it is clear that BF_2 is most influenced by ϵ which depends on the last certain sighting. This result suggests that Model 2 inference is particularly sensitive to when the last certain sighting occurs.

The next section will illustrate this possibility using the same example that we studied with Model 1 case 2, which assumes that there are certain sightings from 1 to 8 and uncertain sightings from 5 to 30 for 35 years.

From inspecting at Fig. 9, it is clear that the peak is exactly at the last certain sighting (t_L). Also by examining the magnitudes of the y-axis, it is clear that BF_2 is more influenced when $\omega < 0.8$. This property of Model 2 is responsible for the prediction that the species is extant only if the last certain sighting and the observation end period are close to one another.

The steep peak at the last certain sighting can be explained in the same way as for the first model.

When $x = t_L/T$ and $n(xT) = n_1$, we obtain

$$\begin{aligned} BF_2 &= \int_\epsilon^1 \int_0^1 \frac{(1-\omega)^{n_u - n_1}}{\omega^{n_u}(\frac{t_L}{T})^{n_c}(\frac{t_L}{T}+\frac{1}{\omega}-1)^{n_U}} d\omega dx \\ &= \int_\epsilon^1 \int_0^1 \left[\frac{(1-\omega)^{1-\frac{n_1}{n_u}}}{\omega\left(\frac{t_L}{T}\right)^{\frac{n_c}{n_u}}\left(\frac{t_L}{T}+\frac{1}{\omega}-1\right)}\right]^{n_u} d\omega dx. \end{aligned} \tag{25}$$

A steep peak will occur when $\omega = \omega_2$ and

$$(1-\omega_2)^{1-\frac{n_1}{n_u}} = \omega_2\left(\frac{t_L}{T}\right)^{\frac{n_c}{n_u}}\left(\frac{t_L}{T}+\frac{1}{\omega_2}-1\right). \tag{26}$$

Solving Eq. (26) with the assumed data it was found that $\omega_2 = 0.79$. By observing Fig. 9, it is clear that the peak at the last certain sighting begins to increase rapidly when $\omega < 0.8$.

By the results of Eq. (26), it is clear that the second method is sensitive to the last certain sighting. The distance between the last certain sighting and the observation end period will determine the value of BF_2.

7. Guideline to select between models

Solow and Beet (2014) emphasized that the choice of model depends on the understanding of what they called the natural history of the sighting record. For the particular case of the Ivory-billed Woodpecker, they pointed out that the second model is appropriate based on natural history - certain sightings were based on physical specimens, uncertain sightings on calls.

Our results show that Model 1 is sensitive to the last uncertain sighting while Model 2 is sensitive to the last certain sighting. The choice of model will obviously depend on the reliability of the uncertain sightings in the observed data. This can be investigated by exploring the posterior probability density function (PDF) of the parameter Ω which represents the expected proportion of valid sightings and is a measure of the quality of uncertain sightings (Solow et al., 2012). If Ω is near one, then most of

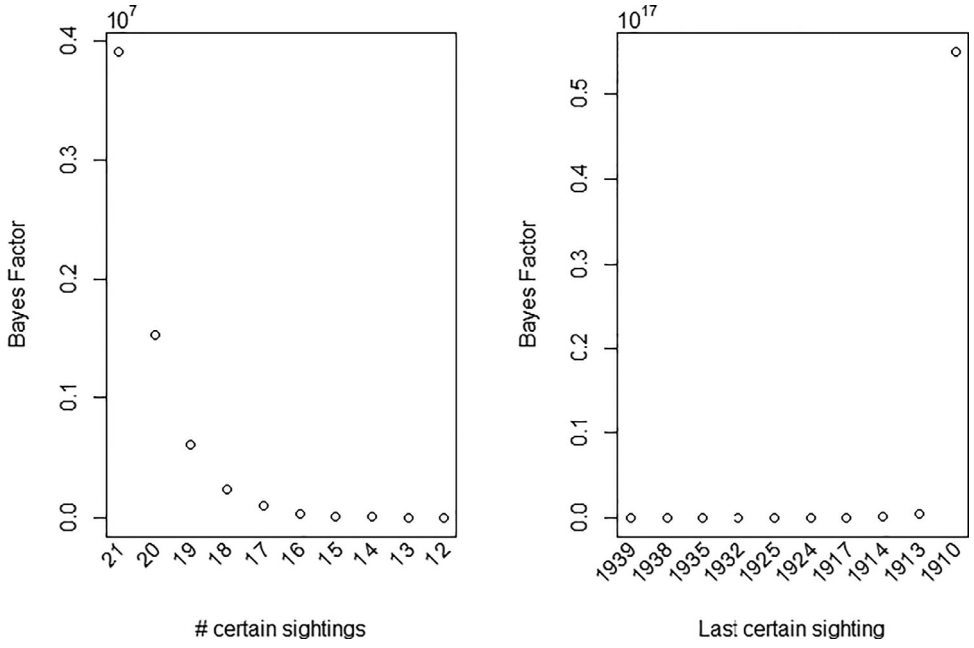


Fig. 8. Change in Bayes factor for Model 2 for different variants in certain sightings. RH graph shows a much more sensitivity in Bayes Factor compared to the LH graph which provides evidence of Model 2 being sensitive to the last certain sighting.

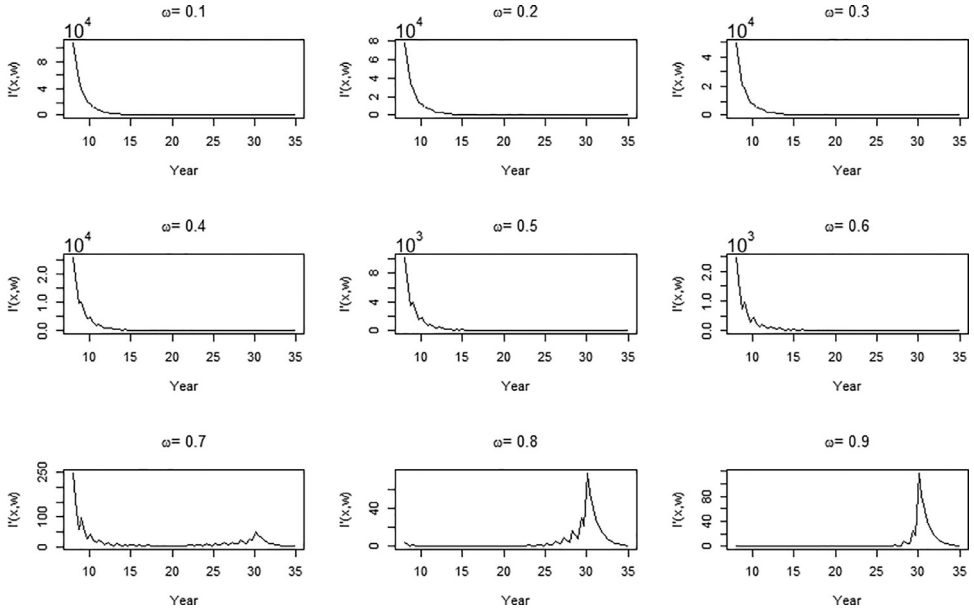


Fig. 9. $I'(\omega, x)$ as a function of time for different fixed values of ω when sightings are homogeneous. As in Fig. 5 ω is the expected proportion of valid sightings but $I'(\omega, x)$ represents the integrand in Eq. (22) which is used to calculate Bayes factor for Model 2. In here $I'(\omega, x)$ shows an opposite behavior compared to $I(\omega, x)$ by having its major peak at the last certain sighting. Also note that this peak gradually decrease when ω is increased.

the uncertain sightings prior to extinction are valid. If Ω is near zero, this suggests that most of the uncertain sightings prior to extinction are invalid.By examining the posterior PDF of we can gain useful information as to whether Model 1 or Model 2 is the correct model to use.

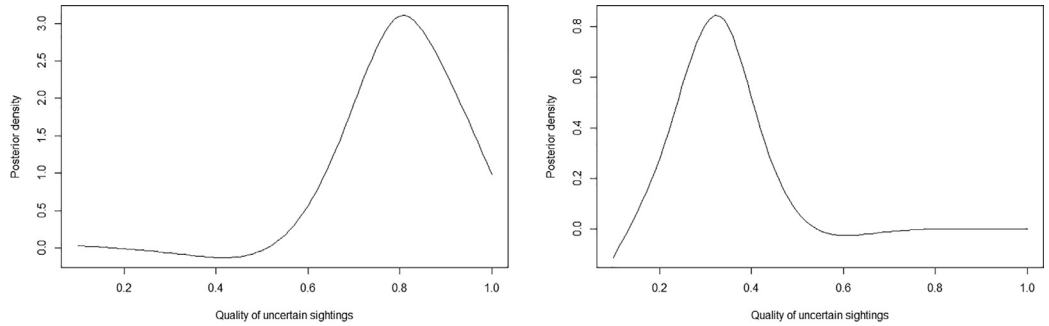
The posterior PDF of Ω is Solow et al. (2012):

$$p(\omega|t) = \frac{p(t|\omega)}{\int_0^1 p(t|\omega)d\omega} \tag{27}$$

where

$$p(t|\omega) = \begin{cases} \int_{t_L}^{T} \omega^{-n_u}(1-\omega)^{n-n(\tau_E)}(n-1)! \\ \quad \times(\tau_E + (\frac{1-\omega}{\omega})T)^{-n} p(\tau_E)d\tau_E, & \text{Model 1} \\ \int_{t_L}^{T} (n_c-1)!\tau_E^{-n_c}(n_u-1)!\omega^{-n_u}(1-\omega)^{n_u-n_u(\tau_E)} \\ \quad \times\left(\tau_E + \left(\frac{1-\omega}{\omega}\right)T\right)^{-n_u} d\tau_E. & \text{Model 2} \end{cases} \tag{28}$$

Solow and Beet (2014). By comparing the posterior PDF of Ω with the realistic expectation of the validity of uncertain sightings one can choose the appropriate model to make inferences i.e., Model 1 or Model 2. To illustrate this idea we generated the two



(a) Model 1 (b) Model 2

Fig. 10. Posterior PDF of parameter Ω, which is a measure of the quality of uncertain sightings. The LH graph indicates that most uncertain sightings prior to extinction tend to be valid under Model 1. The RH graph indicates that under Model 2 most uncertain sightings are invalid.

posterior distributions related to each model for the Ivory-billed Woodpecker data, as shown in Fig. 10.

Fig. 10 indicates that, prior to extinction most uncertain sightings are valid under Model 1 which makes Model 1 to be sensitive to the uncertain sightings. Under Model 2 most uncertain sightings are invalid prior to extinction which makes certain sightings become the dominating factor. As a rule of thumb, our findings suggest that if most of the uncertain sightings are known to be valid Model 1 is appropriate, on the other hand if most of the uncertain sightings are known to be invalid Model 2 is appropriate.

There might also be situations where the validity of uncertain sightings is not known. In this case selecting one model over the other will be risky because of this ignorance of model uncertainty. In such situations there might be a need to consider Bayesian Model Averaging, which would examine the response of a weighted average of the two models. We hope to treat such an approach in future work.

8. Discussion

In this article, we study the sensitivities of the two important models proposed by Solow and Beet (2014) for predicting extinction, in terms of the particular characteristics of the historical sighting records of the species under investigation. The differences between the two models can be understood visually by comparing Figs. 2 and 6. We mathematically explain and give reasons for the different results obtained from the two models, when both are used to analyze the same data set. As seen in the results section and in Solow and Beet (2014), it is clear that the two models behave differently. A simple way of conceptualizing the difference is by noting that, at least until the time the species goes extinct, Model 1 is framed in terms of the underlying valid and invalid sightings occurring as different but stationary Poisson processes (at constant rates Λ and Θ respectively).

After the species goes extinct, all sightings are invalid. (Note that valid sightings consist of certain and valid uncertain sightings.) A relatively high rate of certain sightings before t_L ensures that the rate of valid sightings is large. Thus after t_L, most of the uncertain sightings should be valid in order to maintain the same valid sighting rate. Hence the last uncertain sighting is more influential on Model 1, as compared to the last certain sighting t_L.

In contrast, at least until the species goes extinct, Model 2 is framed in terms of the underlying certain and uncertain (valid\invalid) sightings occurring as different stationary processes (at constant rates M and $\Lambda + \Theta$ respectively). After the species goes extinct all sightings are uncertain and must also be invalid. A relatively high rate of certain sightings before t_L, and total absence of them afterwards, makes the last certain sighting t_L directly related to the extinction time (as pointed out by Solow and Beet (2014). This helps explain our finding that Model 2 is particularly sensitive to the last certain sighting t_L.

As discussed, the two models show two different ways of taking errors in the sighting data into account. One focuses on the validity and invalidity of the sightings (Model 1), whereas the other focuses on the certainty and uncertainty of sightings (Model 2). These are subtly different things, yet they can have enormous consequence. In general, we only know whether data points are certain or uncertain, yet Model 1 shows that this might not be sufficient information. This is because we rarely have information as to the validity or invalidity of uncertain sightings, which would be needed if Model 1 were true.

All these characteristics makes model selection more complex because in reality we do not know if the certain and valid uncertain sightings follow different independent Poisson processes (as would be needed in Model 2) or as a single process (Model 1). For instance, consider the no extinction baseline scenario discussed under Model 1, Case 1, which assumes that there are uniformly spread uncertain sightings throughout the observation period. As an example, assume that there are 5 consecutive certain sightings followed by 25 consecutive uncertain sightings. If one is interested in finding out whether or not the species is extinct by the time of the last uncertain sighting at $T = 30$, the choice of model will give two different inferences. Specifically, Model 2 will favor extinction while Model 1 will favor the species being extant. In a special case, if in reality most of the uncertain sightings were truly valid, the inference made under Model 2 would be incorrect. However, if most of the uncertain sightings were truly invalid, then the inference made under Model 1 would be incorrect. Thus which model to be used in which situation is still open for debate as long as the quality of uncertain sightings remains unknown.

Competing interests. We declare we have no competing interests.

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Appendix A

Peak at t_{n-1} is less than the peak at t_n which is shown mathematically in the following section.

When $x = (t_n - 1)/T$ and $n(xT) = n - 1$, we have the following

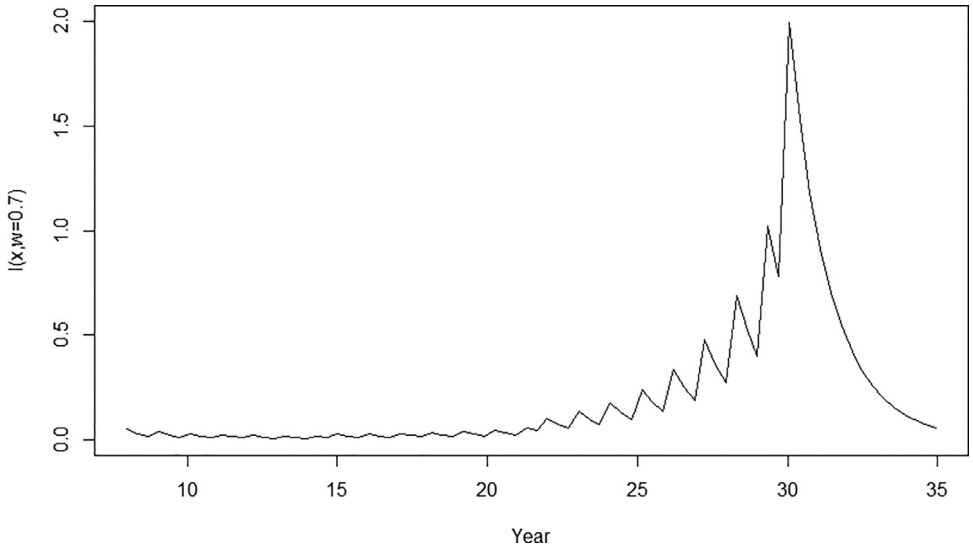

Fig. A.11. $I(\omega, x)$ as a function of time $\omega = 0.7$.

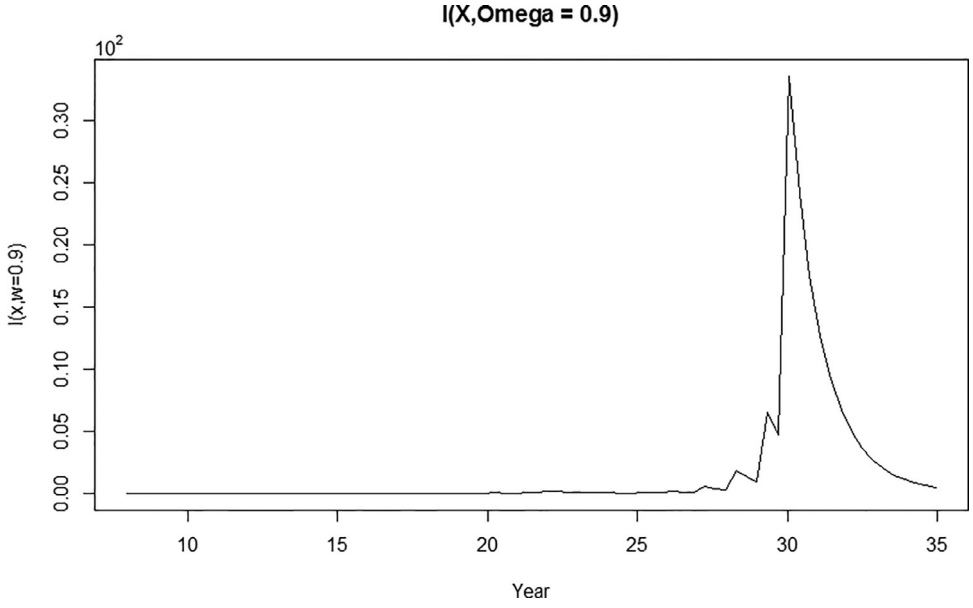

Fig. A.12. $I(\omega, x)$ as a function of time for a fixed values of $\omega = 0.9$ when sightings are non-homogeneous at middle.

$$
\begin{aligned}
BF_1 &= (n_c+1)\int_{\epsilon}^{1}\int_{0}^{1}\omega^{n_c-n}\frac{(1-\omega)^{n-n(xT)}}{(x+\frac{1}{\omega}-1)^n}d\omega dx \\
&= (n_c+1)\int_{\epsilon}^{1}\int_{0}^{1}(1-\omega)\left[\frac{\omega^{n_c/n}}{\omega\left(\left(\frac{t_{n-1}}{T}\right)+\left(\frac{1}{\omega}\right)-1\right)}\right]^n d\omega dx \\
&\approx (n_c+1)\int_{\epsilon}^{1}\int_{0}^{1}(1-\omega)\left[\frac{\omega^{n_c/n}}{\omega\left(\left(\frac{t_n}{T}\right)+\left(\frac{1}{\omega}\right)-1\right)}\right]^n d\omega dx \quad \text{(A.1)}
\end{aligned}
$$

Note that (t_{n-1}/T) can be approximated by (t_n/T) as sightings are homogeneous.

Comparing Eq. (A.1) with Eq. (14), it is clear that at t_{n-1}, the peak is different by a factor of $(1-\omega)$, approximately. Consider the case where $\omega = 0.7$, the plot of $I(\omega, x)$ confirms that the peak at $t_{n-1}$is approximately different from t_n by a factor of $(1-\omega)$

By the results of Fig. A.11, it is clear that the peak at $t_{n-1}$is smaller than the peak at t_n when sightings are homogeneous.

Case 3: Last uncertain sighting $t_n < T$ with non-homogeneous sightings at middle of the sightings

It will be assumed that there are certain sightings in every year from 1 to 8 and uncertain sightings from year 5–22, 25–30 for the 35 years of the observation period. Fig. A.12 illustrates the plot of the integrand $I(\omega, x)$ at a fixed value of $\omega = 0.9$, as a function of time x. $\omega = 0.9$ was chosen as it gives a clear idea where the peak is located this can be verified by Fig. 5.

Similar to Case 1, the integrand has a major peak order of magnitude higher than 1.5 and it is exactly located at the last uncertain sighting (t_n) not before or after it.

Case 4: Last uncertain sighting $t_n < T$ with non-homogeneous sightings at end of the sightings

It will be assumed that there are certain sightings in every year from 1 to 8 and uncertain sightings from year 5–25, 30 for the 35 years of the observation period. Fig. A.13 illustrates the plot of the integrand $I(\omega, x)$ at a fixed value of $\omega = 0.9$, as a function of time x.

Fig. A.13 makes clear that for $\omega > 0.6$, the integrand has a major peak orders of magnitude higher than 10 and it is not exactly located at the last uncertain sighting (t_n), in fact its located at where

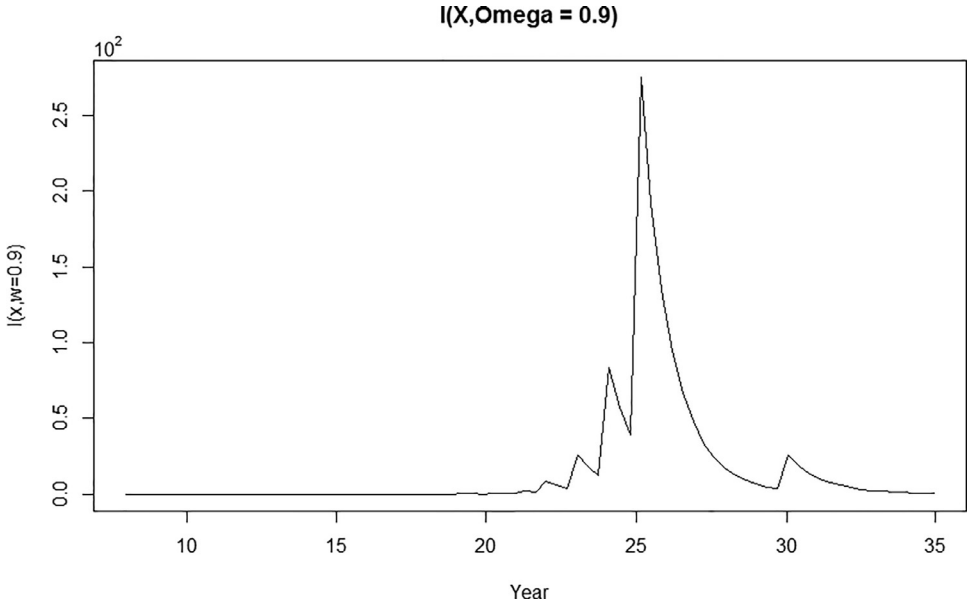

Fig. A.13. $I(\omega, x)$ as a function of time for a fixed values of $\omega = 0.9$ when sightings are non-homogeneous at end.

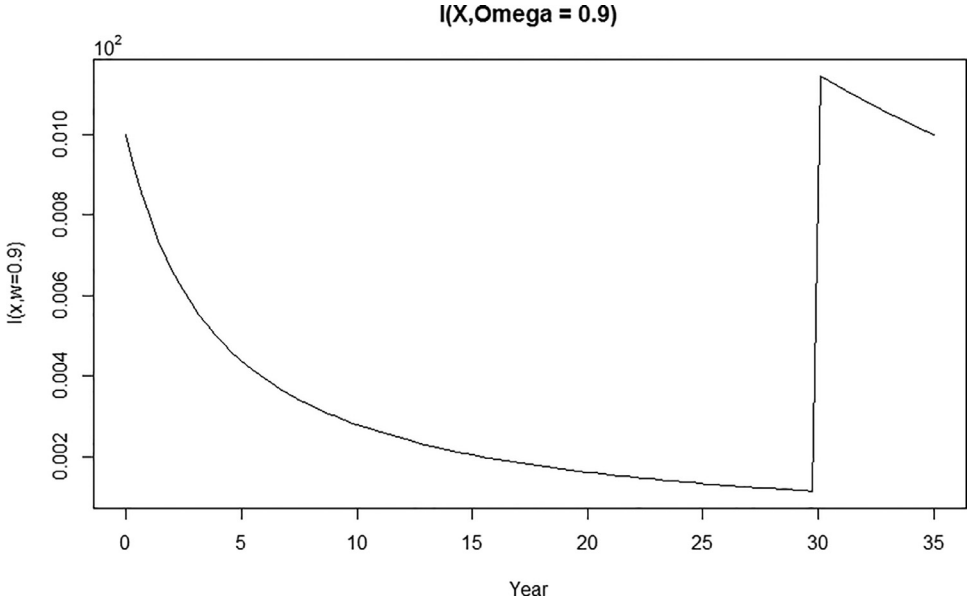

Fig. A.14. $I(\omega, x)$ as a function of time for a fixed values of $\omega = 0.9$ when there is only one uncertain sighting.

the non-homogeneity occurs (t_{n_1}). This could be farther explained by Eq. (A.2).

When $x = \frac{t_{n-1}}{T}$ and $n(xT) = n - 1$, we get

$$BF_1 = (n_c + 1)\int_{\epsilon}^{1}\int_{0}^{1} \omega^{n_c - n}\frac{(1-\omega)^{n-n(xT)}}{(x + \frac{1}{\omega} - 1)^n} d\omega dx$$

$$= (n_c + 1)\int_{\epsilon}^{1}\int_{0}^{1}\left[\frac{\omega^{n_c/n}}{\omega\left(\left(\frac{t_{n-1}}{T}\right) + \left(\frac{1}{\omega}\right) - 1\right)}\right]^n d\omega dx. \qquad (A.2)$$

Now $(\frac{t_{n-1}}{T})$ cannot be approximated by $(\frac{t_n}{T})$ as sightings are non-homogeneous at the end. This result in $(\frac{t_{n-1}}{T}) \ll (\frac{t_n}{T})$, hence the integrand will have a maximum at (t_{n-1}).

Case 5: When there is only one uncertain sighting and assuming that the species was extant at the start of observation (i.e certain sighting at 0)

It will be assumed that there is only one uncertain sighting in 30 for the 35 years of the observation period. Fig. A.14 illustrates the plot of the integrand $I(\omega, x)$ at a fixed value of $\omega = 0.9$, as a function of time x.

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